BUDDING TENTACLES OF GONIONEMUS.

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While looking over specimens of *Gonionemus* for class work, and being somewhat on the lookout for any cases of variation, etc., my attention was arrested by an unusual appearance of a tentacle. Near the distal end was present a small knob which at first glance appeared simply as a protuberance, apparently without any very definite form or structure.

On further and more careful examination it seemed to me to warrant a careful study. It was somewhat similar to some of the conditions found by Hargitt[1] in his work on the variation of

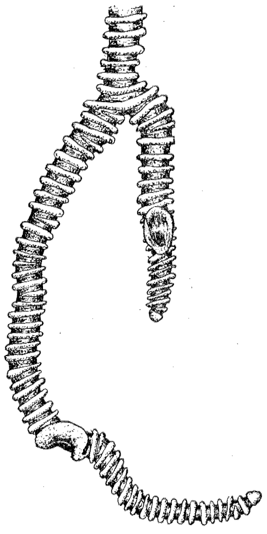

FIG. 1.

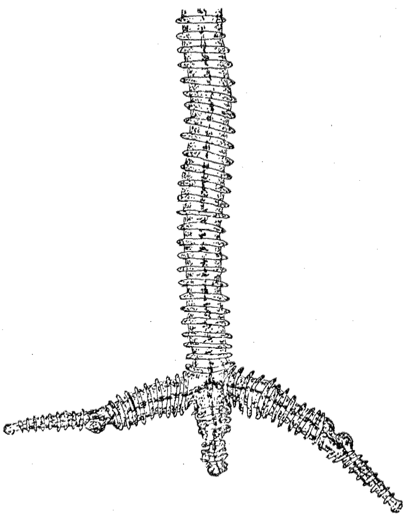

FIG. 2.

this form. The conditions referred to are the presence of bifurcated tentacles. He found a number of tentacles which had double, or in one case triple tips. In all these cases the extra tip or bud seemed to arise either from the suctorial pad or else immediately proximal to it. Fig. 1 represents a rather typical example of bifid tentacle. The specimen is one I found in C.

[1] "Variation among Hydromedusæ," BIOL. BULL., Vol. II., No. 5, 1901.

W. Hargitt's collection, but which he did not use in his paper on variation. The extra tip is seen to be much shorter than the main tip. Each tip is supplied with one of the suctorial pads, but the shorter one arises from a point considerably proximal to the pad on the main tentacle and directly from the tissue of the tentacle. No sign of injury is present. The appearance of this tentacle suggests the probable result of further growth of the bud shown in Fig. 3, except of course the lack of the pad at the base of the bud. Fig. 2, showing a trifid tentacle, is taken from Hargitt's paper on variation (*op. cit.*). It shows two branches arising from near the end of the main tentacle which seems to be degenerate as mentioned later. The buds here do not seem to arise from the suctorial pad of the main tentacle, which is not shown, but each bud is supplied with a pad near its tip. The knob on the tentacle under consideration, however, had more the appearance of a bud than a bifurcation. This was due chiefly to its small size which rather suggested that it was a very early stage in the formation of an extra tip to the tentacle.

The bud arose from a definite base which presented almost exactly the same external appearance as the normal suctorial pad. This similarity consisted not only in the smooth appearance, due to the absence of the ectodermal ridges found on the other parts of the tentacle, but also in its concave form, and the further presence of a bend or "knee" in the tentacle at this point; all of which are characteristic of the normal suctorial pad (Figs. 3–5). The bud arose from a depression in the base (Fig. 4) due to the cup-like shape of the pad already mentioned.

No external sign of injury was found either in this pad or in the surrounding tissue. The pad was of course not functional as an adhesive organ, another functional one being present nearer the distal end of the tentacle (Figs. 3 and 5). Whether this new pad formed after the beginning of the development of the bud from the old pad, whose functional activity would thus be destroyed; or whether a second pad formed first, and a bud began to develop from the old one (which would not then be necessary) simply as a result of the capacity for regeneration, or rather duplication of parts, inherent in the tentacles, is an extremely interesting question. Of course no direct answer can be

made without a considerable body of facts before us, coming from actual observations on this particular point; facts which it would be very difficult if not impossible to obtain. It seems to me, however, that we can suggest a probable answer from conditions observed in other cases, which bear more or less directly on this point. A comparison of Figs. 1 and 2 with some of those in Hargitt's paper show that buds do not always arise from pads. Indeed of the six figures of bifid and trifid tentacles shown in that paper and in this, only two show the bud as arising from the pad. This alone would show quite conclusively that there is no necessary or regular connection between the bud

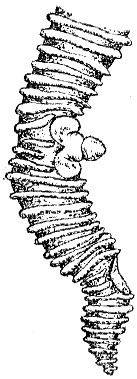

FIG. 3.

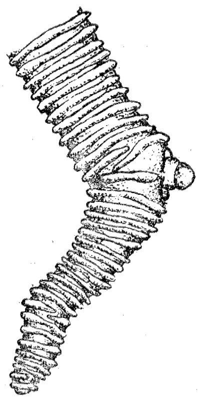

FIG. 4.

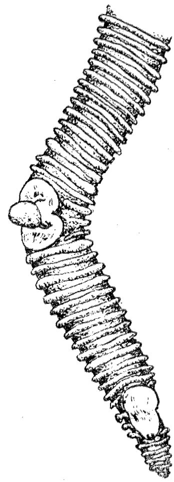

FIG. 5.

and the suctorial pad. This is further emphasized by the fact that I found nine tentacles having each three pads, apparently well developed and functional, and yet there was not the least sign of buds arising from any of the pads. These facts all point directly toward an unusual predisposition to a duplication of organs, and this perhaps offers the most satisfactory explanation of the budding and bifurcation of tentacles.

The bud showed a constriction near its middle region, but did not present externally any signs of annulation, or rather of the ectodermal ridges present on the old tentacle. However, nematocysts were present in abundance. The general appearance of the

bud is similar to that of the old tentacle, with the exception noted above, and is undoubtedly of the same structure.

Hargitt (*op. cit.*, p. 244) in referring to bifid and trifid tentacles suggested that they might have orginataed is the result of some injury to the distal end of the tentacle. This seemed to be especially indicated by the one trifid tentacle found. In this case there seemed to be a degeneration or atrophy of the median branch, which was probably the end of the original tentacle. From the sides of this tentacle two branches arose opposite each other which were considerably longer than the median tip (*cf.* Fig. 2). He says concerning the cause of this: "The degenerating middle tip would very naturally suggest the probability that an injury might have been the predisposing cause of the secondary tips; on the other hand, it must not be overlooked that in each of the other specimens with double tips no such cause seems at all evident."

It was with the thought of trying to determine whether there was any sign of injury which might have influenced the formation of a bud in that region, as well as to determine the histogenic changes involved in its formation, that I was led to undertake a careful study of this budding tentacle.

The tentacle was stained in toto with borax carmine. Sections were cut transversely across the tentacle, thus making the sections of the bud longitudinal.

Fig. 6 represents a section of the entire tentacle showing the bud in its general relations. The entoderm of the bud is seen to be directly continuous with the entoderm of the tentacle. The bud is solid with the exception of a cavity at the distal end and there is no connection between this cavity and the cavity of the tentacle. It will be noticed, however, that the cells are arranged more or less definitely in two rows with the dividing line quite distinctly marked in the proximal region, as though in further growth these would pull apart and thus connect the distal cavity of the bud with the cavity of the tentacle. On either side of the bud are masses of the rather dense tissue which makes up the suctorial or adhesive pad already mentioned. This tissue resembles very much muscular tissue rather than glandular tissue, suggesting that the pad acts by virtue of its muscularity, rather than by

means of a secreted adhesive substance as suggested by Perkins.[1] At the edges of this pad is present the collar-like expansion of the ectoderm which is characteristic of this structure normally. Indeed, the shape, size and contents of these cells, as well as their method of staining and general appearance, is almost exactly the same as in the normal pad. Thus there seems little doubt that there was originally present here a functional suctorial pad. So

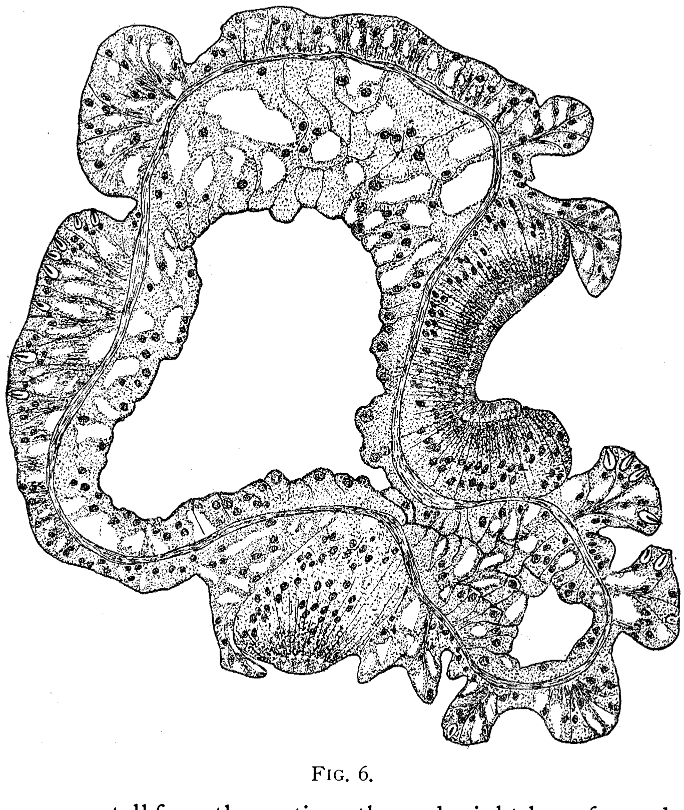

FIG. 6.

far as we can tell from the sections the pad might have formed after the bud began its development, though this is very unlikely, since in such case the function would be quite limited. Indeed the pad would lose its power of functioning normally if the bud increased in size to any extent. The ectoderm of the bud is thrown into the folds or ridges, which are characteristic of the normal tentacles, and nematocysts are limited to these ridges (*cf.* figures).

[1] "The Development of *Gonionema Murbachii*," *Proc. Acad. Nat. Sci.*, Philadelphia, p. 764, 1902.

Figs. 7, 8, 9 show only the bud and the tissues immediately adjoining. The same general features already noted are also seen here. In Fig. 7 the muscular pad on each side of the base of the bud is nearer the same size than in Fig. 6. The relation of the entoderm of the bud and tentacle is shown in about the same way, but the arrangement of the bud entoderm into two rows is not so distinctly marked. In Fig. 8 this arrangement of entoderm is scarcely indicated, the cells being more or less massed together and not showing any apparent regularity. The character of the tissue of the muscular pad is shown better as are also the ectodermal ridges. The cavity at the distal end of the bud

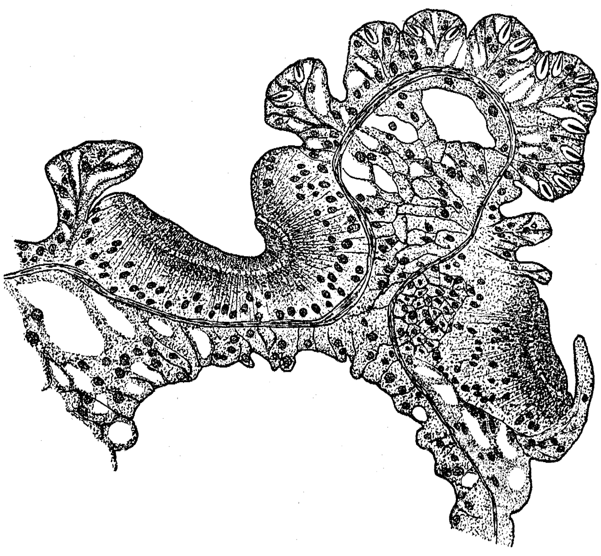

FIG. 7.

is larger than shown in the other figures. In Figs. 8 and 9 the muscular pad is shown on only one side of the base of the bud, showing that the bud is not completely surrounded by it, a feature also indicated in Figs. 3 and 5, where the pad is seen to have a notch or sinus on one side. Fig. 9 represents a section cut one side of the long axis of the bud, so that the entoderm of the bud and tentacle is not continuous.

It will have been noticed that in all the figures the bud is solid with the exception of a cavity at the distal end. Perkins (*op. cit.*, p. 785) referring to the development of the normal tentacle states

that it is at first solid, but that later "the cavity of the circular canal is drawn into it." "The entodermal cells, arranged radially about the central axis, thicken until they are forced away from the center and a tubular cavity is left." This process, he states, begins at the proximal end and the cavity is gradually "carried out along the axis of the tentacle toward the tip." In this bud there seems to be present the cavity at the distal end so

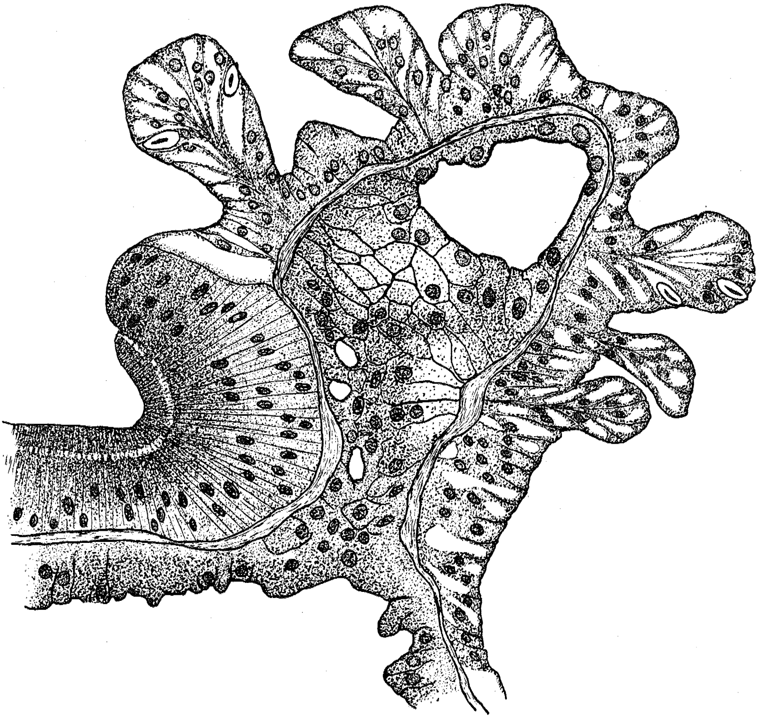

FIG. 8.

that the method just mentioned does not apply, at least not wholly. In Fig. 6 the cells are evidently arranging themselves in rows next the supporting layer, with their edges meeting near the center, suggesting a drawing away from the axis and a formation of a cavity (as Perkins suggests) connecting the cavity of the tentacle with the cavity already formed in the bud. Fig. 9, however, would seem to indicate a somewhat modified process. The cell outlines are not distinct, so that their arrangement cannot be definitely determined, but in the central part of the core are a

number of irregular cavities. This suggests the possibility of these cavities enlarging and running together, the cells at the same time taking up a regular position next the supporting layer, and thus the cavity of the bud being formed. In neither case, however, would the process necessarily begin at the proximal end. Furthermore, it is not quite certain just how the cavity at the distal end of the bud forms, or why it should form so early and not involve the proximal portion of the bud.

In regard to the early method of formation of the bud little can be suggested since it has developed beyond the initial stage. It can be said, however, that not the slightest trace of injury was found, which might be a predisposing cause. Alb. Lang[1] from

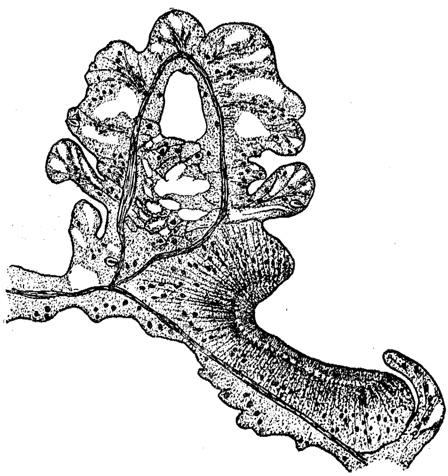

FIG. 9.

his work on budding in *Hydra*, *Eudendrium* and *Plumularia* tried to show that the bud originated from the ectoderm entirely, that the previous view that both layers were active could not be maintained ; ectoderm cells migrated through the supporting layer and formed the bud entoderm, the old entoderm being absorbed. Seeliger[2] and Braem,[3] however, working on *Hydra*, *Eudendrium*, *Plumularia*, *Obelia* and *Sertularella* claimed that Lang's results were entirely incorrect and the conclusions drawn from them

[1] *Zeitschr. f. wiss. Zool.*, Bd. 54, 1892, pp. 365–385.
[2] *Zeitschr. f. wiss. Zool.*, Bd. 58, 1894, pp. 152–188.
[3] *Biol. Centralbl.*, Bd. 14, 1894, pp. 140–161.

not warranted. They found dividing cells in the entoderm as well as in the ectoderm, a condition which Lang did not find. They found no trace of ectoderm cells migrating into the entoderm even in the earliest stages, of the two layers running into each other, of the entoderm being pushed aside and absorbed. Many others also have questioned Lang's claims and maintain that results obtained in many species of hydroids, as well as in other forms of animal life, confirm the old view. My own work on hydroids [1] confirm these results of Seeliger, Braem and others. In working on the regeneration of *Tubularia crocea*, *T. tenella*, *T. larynx*, *Eudendrium ramosum* and *Pennaria tiarella* particular attention was paid to structures which form either wholly or in part by budding. Sections made through these buds in all stages showed none of the features claimed by Lang, such as migrating entoderm cells, dissolution of the supporting layer with the accompanying disappearance of sharp contrast between the two layers, and absorption of the entoderm. Often, usually indeed, the entoderm seemed to be the layer most active in this process. Mitotic division was observed in both ectoderm and entoderm though not abundant, reasons for which are discussed in the above-mentioned paper. Amitotic division was also more or less prevalent in both layers. Perkins (*op. cit.*, p. 784) referring to the formation of the tentacle in *Gonionemus* says the three layers, ectoderm, entoderm and supporting layer "are pushed out somewhat in the growth of the tentacle, the region of greatest activity being the endodermal layer, where the core of the tentacle is formed by a rapid outgrowth of the cells of the body wall accompanied by multiplication of these same cells." He further states that there is not even an initial thickening of the ectoderm in the region where the tentacle is to appear. In regard to budding in the larval form likewise, he states that the ectoderm and entoderm cells divide, the entoderm pushes out gradually, the ectoderm growing so regularly as to cover it with a layer of constant thickness. Thus it has been conclusively proved that budding in many hydroids, as well as in the formation of the tentacle and in other buds of *Gonionemus*, involves both layers, and cells in both layers increase rapidly by division. This would entirely dis-

[1] *Arch. f. Ent-mech.*, Bd., XVII., Heft 1, 1903, pp. 64–91.

credit the universality of Lang's claims, even if they held true for a few forms.

Since this is the method of the formation of the tentacles, and of buds in other regions of *Gonionemus*, we may safely assume that probably the same process would be active in the formation of the bud from the tentacle, or at least to a great extent. Greater support is given this assumption by the fact of the presence of mitotically dividing nuclei found in the entoderm of the bud. They were not definitely determined in the ectoderm though doubtless present.

I am glad to acknowledge my indebtedness to my father, C. W. Hargitt, for permission to reproduce Fig. 2, which appeared in his paper on "Variation among Hydromedusæ," and also for allowing me to examine his collections of *Gonionemus*.

Zoölogical Laboratory, Syracuse University,
January 18, 1904.